STUDIES ON THE MODE OF INHERITANCE OF HAJIRA TYPE STEM RUST RESISTANCE AND VICTORIA TYPE CROWN RUST RESISTANCE AS EXHIBITED IN CROSSES INVOLVING THE OAT VARIETY GARRY.

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[Read 25th May, 1960.]

Synopsis.

Studies on the mode of inheritance of stem rust and crown rust resistance to certain races of the pathogens in crosses involving the resistant oat variety Garry and various susceptible varieties showed that Garry comprised a heterogeneous mixture of genotypes. Three factor pairs conditioning stem rust resistance were identified, designated as Rd_1, an independent gene operative against races 2 and 12, and the linked genes Hj_1 and Hj_2 (with a recombination value of $26{\cdot}69 \pm 2{\cdot}29$ crossover units) conditioning seedling resistance to races 2, 10 and 12 and field inoculum. In all, six factor pairs were concerned with crown rust resistance and these were in three linkage groups. Group 1 comprised three genes with the following estimated linkage values: Vc_a Vc_b $\overline{Vc}_1$ ——————. Vc_a and Vc_b were complementary genes for seedling resistance, whilst $\overline{Vc}_1$ $9{\cdot}59 \pm 1{\cdot}68$ 10 approx. conditioned adult plant resistance only. Linkage group 2 comprised the two genes Vc_2 and IVc_2 with an estimated recombination value of 10 crossover units between them. Vc_2 conditioned seedling as well as adult plant resistance, but was inhibited by IVc_2. Thirdly, $\overline{Vc}_3$ was an independent dominant gene for adult plant resistance only. The genes conditioning stem rust resistance were genetically independent of those for crown rust resistance.

Introduction.

Hajira has been used as a source of resistance to oat stem rust, *Puccinia graminis avenae* E. & H., since 1926. The variety was introduced into North America from Egypt (Welsh and Johnson, 1951). This source of resistance has assumed particular importance since it has conferred resistance against all the existing races in North America and Australia.

Originally Hajira was believed to be resistant only to races 1, 2, 3, 5 and 7, and subsequently also to race 12, which was discovered later. In 1936, however, certain advanced generation lines from the cross Hajira × Joanette were tested in the glass-house to race 6 and certain other races (Welsh, 1936). Resistance to race 6 was observed at low and intermediate temperatures in a few lines. These lines were uniformly resistant to race 8 also and this resistance was thought at that time to have been obtained through transgressive segregation. History of the utilization of this source of resistance has been reviewed by Welsh and Johnson (1951, 1954). Their studies in 1951 indicated that Hajira itself contributed genes for resistance to all the races of stem rust. Four hundred single plant selections of Hajira were tested and 12% showed resistance to all the known races in Canada.

Victoria was introduced into the United States from South America in 1927 (Stanton and Murphy, 1933) and its resistance was incorporated into economic varieties by 1940 (Stanton and Coffman, 1943). To combine both stem rust and crown rust resistances into one variety, Hajira and Victoria were used in a three-way cross, Victoria × (Hajira × Banner) × Victory, made in 1930 in Canada. Promising rust resistant selections were made and of them a few, viz., R.L.1681, R.L.1692 and R.L.2123, are worthy of mention in the present connection. R.L.1692 and R.L.2123 were later named Garry and Rodney respectively.

The variety Garry was originally introduced into Australia under the designation R.L.1692 and later as Garry. Both strains proved to be resistant to all the known races of stem rust in Australia and to all the races of crown rust until 1952, when a race

attacking Victoria was identified (Baker and Upadhyaya, 1955). Workers abroad found that the crown rust resistance of Victoria type was associated with susceptibility to Victoria blight. This disease has been reported in Queensland (Miles and Rosser, 1954) but has not assumed any serious proportions in Australia. Due to its resistance to all the races of stem rust Garry still remains a valuable source of rust resistance.

Associated with a sound breeding programme, a knowledge of the mode of inheritance of rust resistance is very essential. The present studies were undertaken with this object in view.

Literature Review.

Studies on the mode of inheritance of Hajira type of stem rust resistance have been reported by Welsh (1931), Gordon and Welsh (1932), Litzenberger (1949), Kehr and Hayes (1950), Kehr *et al.* (1950), Welsh and Johnson (1951, 1954) and Osler and Hayes (1953).

Welsh (1931) and Gordon and Welsh (1932) reported a monofactorial inheritance of stem rust resistance to races 1, 2, 3, 5 and 7. This was independent of the Joanette factor for resistance to race 4. Foote (quoted by Kehr *et al.*, 1950) and Osler and Hayes (1953) reported that a single factor governed resistance to races 7 and 8 in selections from the crosses Hajira × Joanette and Victoria × (Hajira × Banner). Kehr and Hayes (1950) had indications of the presence of more than one factor for resistance to race 6 in the cross Hajira × Joanette. They obtained a near 13:3 ratio of resistant and segregating to susceptible F_3 families. Litzenberger (1949) found a trigenic segregation in the cross Hajira × Joanette selection × Mindo, against race 8. One of these genes was allelic with the White Russian factor for resistance to races 2 and 8. All the three factors were independent.

Welsh and Johnson (1951) obtained divergent results with different selections from crosses involving Victoria × (Hajira × Banner). Resistance to race 8 in Garry and Canuck was conditioned by a single factor. In the cross of Canuck it was revealed that the same factor conditioned resistance to other races also. Two independently inherited genes in R.L.1681 conditioned resistance to race 8. In the field, one of these genes conditioned resistance to all the twelve races of stem rust, viz., 1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12 and 13. Later studies in 1954 revealed the presence of three independent genes in Garry. Gene "A" conditioned resistance to races 1, 2, 3, 5, 7, 7A and 12; gene "B" to the same races as above except 7A; and gene "C" to races 4, 6, 8, 10, 11 and 13. Other varieties supposed to possess these various factors were: gene "A"—Ajax, Richland, Green Russian and R.L.1574 (selection from Victoria × (Hajira × Banner); gene "B"—Canuck, R.L.1225 (sister selection of R.L.1574), R.L.1574 and Rodney (R.L.2123) and gene "C"—Canuck, R.L.1225, R.L.1574 and Rodney.

The inheritance of the crown rust resistance of Victoria or its derivatives has been studied by Smith (1934), Waterhouse (1939), Weetman (1942), Murphy and Meehan (1946), Litzenberger (1949), Poehlman and Kingsolver (1950), Griffiths (1953) and Welsh, Peturson and Machacek (1954).

The studies by Smith revealed that either more than a single factor was involved or that susceptible types were eliminated due to some type of sterility. From the F_2 studies in the cross Algerian × Victoria against race 6, Waterhouse (1939) concluded that three independent factors governed resistance to this race. Weetman (1942) observed that resistance to races 1 and 45 in Victoria was governed by a single factor. Murphy and Meehan (1946) and Litzenberger (1949), working with highly rust resistant derivatives of Victoria, found only one gene to be responsible for resistance. Griffiths (1953) also reported the presence of only one gene in Victoria for its hypersensitive type of reaction. The observations of Poehlman and Kingsolver (1950), however, indicated the operation of a second factor conditioning an intermediate type of resistance to races 1 and 45. These lines were resistant to Victoria blight. Welsh, Peturson and Machacek (1954) studied crosses involving Garry and R.L.1987 and concluded that the hypersensitive reaction to races 4, 5, 34A and 57 was governed by a single dominant factor. This was linked with susceptibility to Victoria blight.

Resistance to races 1, 2, 3, 6, 24, 34, 38 and 45 was conditioned by three dominant factors. Gene "A" was epistatic to gene "B" and conditioned strong resistance. Gene "B" conditioned susceptibility and was epistatic (inhibitor) to gene "C" which produced a weaker type of hypersensitive reaction and was associated with susceptibility to Victoria blight.

Independence of the factors for stem rust resistance both in Laggan and in Hajira × Joanette selection and Victoria type of crown rust resistance was reported by Waterhouse (1939) and Litzenberger (1949) respectively.

Experimental Procedure.

(*a*) *Materials.*

In 1953 F_2 embryos from certain F_1 plants of the 1952 harvest were made available. Twenty F_1 plant progenies of the cross Algerian × Garry and fifteen of the cross Fulghum × Garry were included. A further four F_0 seeds were from the cross Burke × Garry. The former crosses were made with Garry accession No. O.259 and the latter with No. O.288.[1] Further crosses were attempted by the senior author in 1953 between Laggan and Garry, Gothland and Garry and Joanette and Garry. A history of the parents other than Garry is as follows:

Algerian (O.9)—a selection made by Pridham in 1918 from a hybrid between Algerian and Red Rustproof.

Fulghum (O.54)—an introduction from North America.

Burke (O.106)—a selection from Kherson by Pridham.

Laggan (O.78)—a selection from Kelsall by Pridham.

Gothland (O.230)—introduced from the U.S.A. as an oat smut differential variety.

Joanette (O.233)—introduced from the U.S.A. as an oat smut differential variety. This variety gave a susceptible reaction to races 8 and 10, instead of the "X" type of mesothetic reaction characteristic of Sevenothree and another Joanette strain (O.45) at low temperatures.

The crosses of Garry with Laggan, Gothland and Joanette were made on single plant selections of Garry. Rust races used were:

Stem rust races—2, 10 and 12.

Crown rust races—203Anz.1, 226Anz.1, 230Anz.1, 237Anz.1, 237Anz.4 and 286Anz.1.

The races used in the present studies were either maintained at Sydney University or isolated from field collections. The position with regard to the races of crown rust present in Australia has been discussed by Baker and Upadhyaya (1955). The races of crown rust mentioned above correspond to races 57, 6, 46 (or 103), 1, 6 and 6 respectively on the old set. Since all the races of crown rust, except race 237Anz.4, were classified as Anz.1 types, it is proposed to denote them in subsequence reference by their international numbers only. Race 237Anz.4 will be denoted as 237–4.

(*b*) *Methods.*

The Technique of Inoculation.—F_1 and F_2 seedlings were inoculated by means of an inoculating needle. In F_2 and F_3 tests occasionally heavily rusted pots were brushed onto moistened and rubbed seedlings. The period of incubation varied from about 20 hours in summer to 36 hours in the winter months.

Data on reaction type were usually recorded after 8 to 10 days in the summer and after about 15 days in the winter. When the same hybrid material was studied to more than one race the seedlings were clipped back to about 2½ inches in height and all the leaves showing any pustule development were removed. After 3–4 days with the emergence of the new leaves, inoculation with a second race was carried out. Sometimes a mixture of races was used on the secondary leaves. The mixture of races involved using heavily infected pots of each race and dusting the spores onto the leaves of the hybrid material.

[1] Numbers refer to Sydney University Oat Variety Collection Number.

During the summer months the temperature in the glasshouses frequently reached as high as 90–95°F. During the winter months the temperatures were occasionally as low as 40°F. To overcome these extremes use was made of a light and temperature controlled room from time to time. Also in the winter months the glasshouses were heated to raise the temperature. The temperature in the control room was kept constant at 68 ± 2°F.

In the adult stage in the field, multiplication of the inoculum of stem rust was done by the hypodermic syringe method and that of crown rust by brushing heavily infected leaves of natural inoculum present in the field. On differential tests this natural inoculum during the 1953 and 1954 seasons showed the presence of races 203, 226 and 237 and some of their subraces. Race 10 of stem rust was found to be the prevalent one during this period. Inoculations in the evening followed by overhead irrigation in the morning usually secured a heavy infection of the hybrid material.

In all tests use of spreader rows of Algerian and Burke for crown rust and of Bond and Victoria for stem rust was made. Tests on the adult plants in the F_1 generation in some of the crosses were undertaken in the University plot where natural infection was not found to any appreciable extent. The plants were hypodermically injected with the inoculum of each appropriate race separately and rust reactions recorded on different tillers.

Recording of Rust Reactions.—In the seedling stage reaction types were recorded according to the scales suggested by Stakman, Levine and Bailey (1923) for stem rust and by Murphy (1935) for crown rust. In all tests parental lines were also inoculated; this permitted more critical classification of the intermediate types of reactions in the hybrid material. The different reaction categories designated were as below.

Reaction.	Infection Type. Seedling.	Adult.	Symbol.
Immune	0;	0	I
Highly resistant ..	; to 1=	1−, 1	R
Resistant	1, 1n, 1+, 2−	1+, 2	R
Moderately resistant ..	2n, 3–cn	1 to 3c	MR
Moderately susceptible ..	2+, 2++, 3	3c to 3+	MS
Susceptible	3+c, 4	3+, 4	S

In the F_3 generation, lines were noted as pure breeding or segregating. In the segregating lines, in some cases there was preponderance of susceptible plants and such lines were designated as S:R; others were written as R:S where the number of resistant plants were in excess. In the seedling stage an average of 20 plants in each F_3 line were tested and in the adult stage an average of 40 plants were tested in rows 4′–6′ long sown one foot apart.

In some cases in order to study the F_3 behaviour of F_2 plants only representative samples from each class of F_2 reactions were tested. In order to calculate the expected frequencies in the F_3 in such cases the observed frequencies were calculated to the original F_2 class frequencies.

Designation of Factors for Resistance.—The following method of gene nomenclature was followed in the present paper. Two letters were taken to abbreviate the name of the variety originally found to possess the particular gene (or the most common variety possessing the gene). Complementary factors were symbolized by alphabetical suffixes and individual genes by numerical suffixes. Inhibitor factors were indicated by use of "I" with the suffix of the gene it inhibited. Genes for adult plant resistance only were symbolized by a line over the gene symbol.

Experimental Results.

(A) *Studies on Stem Rust Resistance.*

(*a*) F_1 Reactions.

In Table 1 are given the parental and F_1 reactions of the crosses of Garry with Algerian, Fulghum, Burke, Laggan, Gothland and Joanette, in tests against races 2, 10 and 12 in the seedling stage, in the adult stage (where specifically inoculated) and in the field.

From this table it will be seen that certain seedlings of the crosses Algerian × Garry and Garry × Gothland were not infected and gave (0) type reactions. Five seedlings of the cross Algerian × Garry gave a reaction more resistant than Garry, and four gave a susceptible reaction. Similarly three seedlings out of eleven in the cross Fulghum × Garry gave a susceptible reaction. One seedling each in the crosses Garry × Gothland and Garry × Joanette gave a less resistant reaction than Garry. Out of a total of 37 seedlings of the various crosses tested in the seedling stage to any one of the three races 20 seedlings gave reactions of Garry type indicating complete dominance of the resistance of Garry. Variations in reaction types between fleck (;) and (2) were probably due to variation in environmental conditions. In the adult tests also the reaction of Garry type seemed in general to be fully dominant. However, three F_1 plants out of twelve tested gave a less resistant reaction.

TABLE 1.

Reactions Against Races of Stem Rust of the F_1s and the Parents Used in Crosses Involving Garry.

Parent or Cross.	Seedling Reaction Types to Races.			Adult Plant Reactions to Races.			Field Reactions.
	2	10	12	2	10	12	
Garry[1]	(1−2−) (98%)	(1−2−) (90%)	(1−2−) (98%)	R	MR	R	R (90%)
Algerian	(3+c)	(3+c)	(3+c)	S	S	S	S
Algerian × Garry F_1	4/5(;) 1/5(3+)	1/5(0) 1/5(;) 3/5(1)	1/5(0) 1/5(1) 3/5(3+)	—	—	—	—
Fulghum	(3+c)	(3+c)	(3+c)	S	S	S	S
Fulghum × Garry F_1	3/3(1)	2/4(1) 2/4(4)	3/4(1) 1/4(4)	—	—	—	—
Burke	(1)	(4)	(1)	—	—	R	S
Burke × Garry F_1	—	2/2(2−)	—	—	—	—	4/4R
Laggan	(1)	(4)	(1)	R	S	R	S
Laggan × Garry F_1	—	2/2(2−)	2/2(2−)	R	1/2R 1/2MR	R	1/2R 1/2MR
Gothland	(3+c)	(3+c)	(3+c)	S	S	S	—
Garry × Gothland F_1	—	1/2(0) 1/2(2)	1/1(2−)	R	—	—	—
Joanette	(3+c)	(3+c)	(3+c)	S	S	S	S
Garry × Joanette F_1	1/1(2)	—	1/1(2−)	R	2/2R	1/2R 1/2MR	—

[1] Garry O.259 was heterogeneous against these races. Garry O.288 was resistant. Garry single plant selections 3 and 8 were resistant ((1) type) and moderately resistant ((2−) type) to race 10, respectively.

(*b*) F_2 Segregation.

Since certain F_1 seedlings gave a susceptible reaction, progenies of the different F_1 plants were tested separately in the F_2. Progenies of F_1 plant nos. 5, 7, 8, 9, 12, 13, 19 and 20 of the cross Algerian × Garry and nos. 7 and 10 of the cross Fulghum × Garry gave only 11 resistant plants out of 1,019 tested to any one of the three races used. Progenies of some of these F_1 plants segregated for resistance to crown rust, and the F_1 plants were morphologically alike indicating their hybrid nature. This small percentage of resistant plants observed could, therefore, be due to natural crossing.

Data on the progenies of other F_1 plants indicating the presence of one or more dominant genes are presented in Tables 2, 3 and 4.

It will be seen from Table 2 that the families of these F_1 plants were susceptible to race 10 but segregated for behaviour to races 2 and/or 12. This indicated the operation of a factor for resistance to races 2 and/or 12 only. Out of a total of 463 plants tested against these races (91 plants tested to race 2 in the cross Fulghum × Garry were also tested to race 12 and are not taken into account) 136 were found to be susceptible. A fit to a 3:1 ratio was not very satisfactory (Chi-square for 1 d.f. = 4·700; P value = 0·05–0·02). Later studies, however, confirmed the operation of a single gene against these races. In the field race 10 was most prevalent.

TABLE 2.

Segregation in the Progenies of Certain F_1 Plants of the Crosses Algerian × Garry and Fulghum × Garry, Indicating the Operation of a Single Factor for Resistance to Races 2 and 12 Only.

F_2 Reaction.	Algerian × Garry. F_1 plant no. 1.		Fulghum × Garry.					
			F_1 plant no. 5.			F_1 plant no. 11.		
	Race 2	Race 10	Race 2	Race 12	Field.	Race 2	Race 12	Race 10
Resistant	29	0	98	131	0	66	69	2
Susceptible ..	14	60	39	54	53	25	29	79
Total	43	60	137	185	53	91	98	81

Certain progenies of F_1 plants indicated the operation of linked genes against all the races and in the field. These data are presented in Table 3.

From the data presented in Table 3 it will be seen that out of a total of 3,096 plants tested to the different races 423 were found susceptible. This gave an over-all ratio of 6·32 resistant to 1 susceptible. A heterogeneity test by the method of Brandt and Snedecor (Fisher, 1936) indicated that the data were homogeneous. Chi-square

TABLE 3.

Segregation in the Progenies of Certain F_1 Plants in Crosses Involving Garry Indicating the Operation of Duplicate Linked Factors Against Races 2, 10, 12 and for Field Behaviour.

Cross and F_1 plant no.	Race Used.	F_2 Reaction.		Ratio of R : S.	Chi-square $\left(\frac{D^2}{I}\right)$	Probability.
		Resistant.	Susceptible.			
Algerian × Garry—						
2	2	96	11	8·73 : 1	0·9966	0·5 –0·3
	12	237	38	6·24 : 1	0·0341	0·9 –0·8
	10	175	18	9·72 : 1	3·1313	0·1 –0·05
	Field	184	21	8·76 : 1	1·9556	0·2 –0·1
4	2	208	37	5·62 : 1	0·5604	0·5 –0·3
	12	60	11	5·45 : 1	0·2450	0·7 –0·5
	10	122	17	7·18 : 1	0·1792	0·7 –0·5
	Field	111	25	4·44 : 1	2·5385	0·2 –0·1
6	2	53	5	10·60 : 1	1·3186	0·3 –0·2
10	10[1]	11	3	3·67 : 1	0·2852	0·7 –0·5
11	2	77	8	9·63 : 1	1·3223	0·3 –0·2
14	Field	58	11	5·27 : 1	0·3501	0·7 –0·5
15	Field[1]	16	2	8·00 : 1	0·0032	0·98–0·95
17	Field	47	3	15·67 : 1	2·9281	0·1 –0·05
18	Field[1]	13	2	6·50 : 1	0·00001	1·00–0·99
Fulghum × Garry—						
3	Field[1]	20	3	6·67 : 1	0·0031	0·98–0·95
6	12	54	6	9·00 : 1	0·6685	0·5 –0·3
9	10[1]	15	2	7·50 : 1	0·0194	0·9 –0·8
12	2 & 12	38	7	5·43 : 1	0·1653	0·7 –0·5
	10	198	35	5·66 : 1	0·4837	0·5 –0·3
13	Field	63	15	4·20 : 1	1·9552	0·2 –0·1
14	Field	44	4	11·00 : 1	1·2370	0·3 –0·2
15	10	68	13	5·23 : 1	0·4456	0·7 –0·5
	Field	158	29	5·85 : 1	0·2070	0·7 –0·5
Garry × Gothland						
2	10	183	35	5·29 : 1	1·2042	0·3 –0·2
5	2	78	11	7·09 : 1	0·0912	0·9 –0·8
Garry × Joanette						
2 and 3	10	159	26	6·12 : 1	0·3656	0·7 –0·5
3 and 4	10	127	25	5·08 : 1	1·0993	0·3 –0·2
Total	.. ..	2673	423	6·32 : 1	0·1295	0·8 –0·7

[1] Yates' correction factor applied.

values for a monogenic and a digenic segregation (3:1 and 15:1) were 212·3 and 272·1 respectively, indicating very large deviations. This intermediate ratio, therefore, suggested the operation of linked duplicate factors.

The operation of a gene for resistance to races 2 and 12 only has already been indicated in the progenies of certain F_1 plants. Further evidence of the presence of this gene was obtained from the segregations in the progenies of certain other F_1 plants. The data are presented in Table 4.

Progenies of three F_1 plants of the cross Fulghum × Garry showed ratios higher than 6·32:1 or 15:1. An aggregate of these three plants, viz., 3, 8 and 15, gave a ratio approximating 31·6:1. Based on the expected segregation of two linked factors and the third factor for resistance to races 2 and 12, the observed ratio was close to the expected ratio of 28·8:1. The expected ratio of 15:1 in the case of F_1 plant 1 was deduced from F_3 studies made later. This ratio indicated the operation of only one of the two linked duplicate factors independent of the factor for resistance to races 2 and 12.

TABLE 4.

Segregation in the Progenies of Certain F_1 Plants in Crosses Involving Garry Indicating the Operation of the Gene for Races 2 and 12 Only in Addition to the Gene or Genes for Resistance to All the Races.

Cross and F_1 plant no.	Race Used.	F_2 Reaction.		Ratio of R : S.	Expected Ratio.	Probability.
		Resistant.	Susceptible.			
Fulghum × Garry						
1	2	171	18	9·50 : 1	15 : 1	0·1–0·05
3	2[1]	97	1	97·00 : 1	96·64 : 3·36	0·5–0·3
8	12	140	7	20·00 : 1	96·64 : 3·36	0·3–0·2
15	12[1]	79	2	39·50 : 1	96·64 : 3·36	0·9–0·8
Burke × Garry	12	354	—		No seg.	
	10	96	26	3·70 : 1	3 : 1	0·5–0·3
	Field	188	63	2·98 : 1	3 : 1	1·0–0·99

[1] Yates' correction factor applied.

In the cross Burke × Garry it will be observed that there was no segregation against race 12 and monogenic segregation against race 10 and in the field. This indicated the presence of a common factor in Garry and Burke for resistance to races 2 and 12 (since Burke was resistant to these two races). A monogenic segregation ratio against race 10 indicated the operation of one of the two linked duplicate factors. In another cross between Garry and Laggan 164 plants were tested against race 12 and of these 10 were found to be susceptible. Since Laggan possessed the gene for resistance against races 2 and 12, Garry single plant selection 8 (which was used in the cross with Laggan) contributed the other gene. F_3 studies to be reported later showed that the gene from Garry conditioned resistance to race 10 also and was independent of the gene in Laggan.

(*c*) Breeding Behaviour in the F_3 Generation.

F_2 progenies of certain F_1 plants indicated the operation of duplicate linked factors for resistance to all three races. F_3 behaviour was studied in the progenies of F_1 plant nos. 6 and 17 of the cross Algerian × Garry and nos. 4 and 8 of the cross Fulghum × Garry. The data are presented in Table 5. Breeding behaviour of 622 resistant plants from F_1 plant progenies indicating operation of duplicate linked factors were also studied to the different races.

In order to calculate the percentage recombination between the linked factors a combined analysis of the F_2 and F_3 data was undertaken utilizing the data presented in Tables 3 and 5. The derived maximum likelihood expression was 2673 Log. $(3+2p-p^2)$ + 455 Log. $(1-2p+p^2)$ + 110 Log. $(1+2p-p^2)$ (Mather, 1938).

Maximization with respect to "p" gave a value of 0·266884 and the variance of "p" calculated from the equation $\frac{1}{s^2p} = \frac{d^2L}{dp^2}$ was ± ·0229. Thus a recombination value of 26·69 ± 2·29 was indicated. On this basis the expected frequencies in the F_2 generation

TABLE 5.

F_3 Reactions of F_2 Plants from the Progenies of Certain F_1 Plants in the Crosses Algerian × Garry and Fulghum × Garry Indicating the Operation of Two Linked Duplicate Factors Only.

(Expected behaviour, 36·56 : 50·00 : 13·44 for Res. : Seg. : Sus. respectively.)

Cross and F_1 plant no.	Race Used.	F_3 Reactions.			Total.	Probability.
		Resistant.	Segregating.	Susceptible.		
Algerian × Garry						
6	12	33	43	11	87	0·98–0·95
17	10	21	22	3	46	0·3–0·2
Fulghum × Garry						
4	10	21	31	7	59	0·9 –0·8
8	10	35	39	11	85	0·7– 0·5
Total	..	110	135	32	277	0·5 –0·3
Lines from resistant F_2 plants only	..	285	377	—	622	0·7 –0·5

were 86·56:13·44 (6·44 Res.:1 Sus.) and in the F_3 were 36·56:50·00:13·44 (Res.:Seg.:Sus.). The repulsion phase heterozygotes were included in the segregating class. For determining the heterogenity Chi-squares for the combined data the equation Chi-square = $\frac{D^2}{I}$ was used. Here "D" was the deviation from the expected and "I" the information about "p". "I" was calculated as the second derivative of the logarithmic likelihood expression. The total Chi-square value was 26·8087 for 30 d.f. The probability value between ·5 and ·3 indicated a good agreement of the data with the hypothesis.

It was observed that the segregation of some progenies in F_2 indicated the additional operation of the factor for resistance to races 2 and 12 only. The breeding behaviour of such progenies is given in Table 6.

It will be seen from Table 6 that in F_1 plant nos. 1 and 2 of the cross Fulghum × Garry and in the crosses Burke × Garry and Laggan × Garry a single gene was responsible for resistance to race 10. In the former two F_1 plants two factors conditioned

TABLE 6.

F_3 Reactions in the Crosses of Garry Indicating the Presence of the Additional Gene for Resistance to Races 2 and 12, and of One or Both Factors for Resistance to Race 10.

Cross and F_1 plant no.	Race Used.	F_3 Reactions.			Total.	Expected Ratio.	Probability.
		Resistant.	Segregating.	Snsceptible.			
Fulghum × Garry							
1 ..	12	25	32	—	57	7 : 8	0·7 –0·5
	10	6	13	6	25	1 : 2 : 1	0·98–0·95
2 ..	2	14	20	1	35	7 : 8 : 1	0·7 –0·5
	12	11	16	—	27	7 : 8 : 1	0·5 –0·3
	10	13	23	10	46	1 : 2 : 1	0·9 –0·8
3 ..	2	33	15	2	50	(*a*)[1]	0·98–0·95
	12	99	36	3	138	(*a*)	0·5 –0·3
	10	19	28	6	53	(*b*)[1]	0·9 –0·8
8 ..	2	18	9	2	29	(*a*)	0·9 –0·8
	12	17	10	2	29	(*a*)	0·9 –0·8
	10	35	39	11	85	(*b*)	0·7 –0·5
9 ..	2	10	6	—	16	(*a*)	0·98–0·95
	12	11	6	—	17	(*a*)	1·0 –0·99
	10	6	8	2	16	(*b*)	1·0 –0·99
Burke × Garry							
1 and 2 ..	10	50	104	47	201	1 : 2 : 1	0·9 –0·8
Garry × Laggan							
1 and 2 ..	10	19	46	20	85	1 : 2 : 1	0·8 –0·7

[1] The ratios expected in (*a*) and (*b*) were 65·55 : 31·09 : 3·36 and 36·56 : 50·00 : 13·44 respectively.

resistance to races 2 and 12. In the F_2 segregation reported earlier in the crosses of Garry with Laggan and Burke the operation of the gene for resistance to races 2 and 12 was evident.

F_3 reactions in the F_1 plant progenies 3, 8 and 9 of the cross Fulghum × Garry clearly indicated the operation of three factors against races 2 and 12 and of two linked factors against race 10. Since for reactions to races 2 and 12 the plants heterozygous for the three factors (both in coupling and in repulsion phases), which are about 37·5% of the lines heterozygous for reactions to race 10, are expected to show less than one susceptible plant in 30 plants, such lines may not be realized in F_3 tests with about 20 seedlings. This class was, therefore, included with the resistant class for working out the expected ratio against races 2 and 12.

TABLE 7.

Relationship between Reactions to Different Races on Identical F_2 Seedlings.

Reactions to Race 12.	Reactions to Race 2.		Reactions to Race 10.		Field Reactions.	Reactions to Race 10.	
	Resistant.	Susceptible.	Resistant.	Susceptible.		Resistant.	Susceptible.
Resistant ..	337	2	217	3	Resistant ..	94	—
Susceptible	3	53	—	27	Susceptible	—	24

(*d*) Relationship of Reactions to Different Races.

(i) F_2 vs. F_2: In Table 7 are given the reactions against two races obtained on the same F_2 plants of the various crosses combined together.

It will clearly be seen from the data presented in Table 7 that the reactions to races 2, 10 and 12 were governed by the same gene. Out of 642 plants studied to these races, only eight plants did not conform to their original reactions. They were resistant to one race, but susceptible to the other. They were probable errors in classification or tagging. The reactions to race 10 and reactions in the field were also perfectly

TABLE 8.

Breeding Behaviour of F_3 Lines from F_2 Plants Classified for Behaviour to Different Races of Stem Rust.

F_3 Behaviour to Races 2 or 12.	F_2 Reaction to Races 2 or 12.		F_2 Reaction to Race 10 or in the Field.	
	Resistant.	Susceptible.	Resistant.	Susceptible.
Resistant	194	(1)	31	3
Segregating ..	146	(1)	19	11
Susceptible	(1)	37	—	4
Race 10.				
Resistant	61	(1)	40	—
Segregating ..	82	(1)	44	(1)
Susceptible	16	7	—	10

Lines shown in brackets were those not expected.

correlated, indicating the operation of the same factor. In the progeny of F_1 plant no. 15 of the cross Fulghum × Garry it was observed that out of 78 plants resistant to race 12, 11 plants were susceptible to race 10. Two plants were susceptible to both races. This indicated the operation of the additional factor for resistance to races 2 and 12 only.

(ii) F_2 vs. F_3: Progenies of a few selected F_1 plants were used for the study of their correlated F_2 and F_3 reactions. The results are presented in Table 8.

It will be seen from Table 8 that only progenies of 6 F_2 plants out of 711 classified did not behave as expected. These were almost certainly errors in classification or

labelling. Similar minor errors were noticed in the behaviour of the F_2 generation. The operation of the gene for resistance to races 2 and 12 only was again noticed. Out of 18 plants classified as susceptible to race 10, 3 gave fully resistant progenies, 11 gave segregating progenies and 4 gave susceptible progenies. A good fit to a 1:2:1 ratio was obtained. Similarly 16 plants classified as resistant to race 2 or 12 gave susceptible progenies to race 10 and 7 were susceptible to both. A fit to a 3:1 F_2 ratio was good.

(iii) F_3 vs. F_2: It was indicated earlier that, due to the operation of three factors for resistance to races 2 and 12 in some lines, less than one plant in 30 was expected to be susceptible. In tests with the two races on separate seedlings such lines may show susceptible reactions to one or other race. Out of 125 lines tested to both races from such material, 56 were resistant to both, 46 were segregating and 6 were susceptible. However, 8 lines resistant to race 12 showed segregation to race 2 and 9 lines showed a reciprocal behaviour. From the progenies of certain F_1 plants showing the presence of the gene for resistance to races 2 and 12 and also genes for resistance to race 10, 32 lines susceptible to race 10 were tested for their reactions to races 2 and 12. In these, 8 resistant, 17 segregating and 7 susceptible lines were observed. The good fit to a 1:2:1 ratio indicated the independence of this factor from the factors for resistance to all races.

Notes taken on the F_3 lines for stem rust reactions in the field were not satisfactory because of a low incidence of stem rust in this material. It was, however, observed that all lines giving a susceptible reaction to race 10 were susceptible in the field with about 15% infection. These results with earlier reported F_2 studies indicated the operation of the same linked factors for adult plant resistance.

(*e*) Designation of Factors for Resistance to Stem Rust.

It has been shown that Garry possessed a gene for resistance to races 2 and 12 only, which was common with the factor in Burke. Since Burke is a sister selection of Richland (a widely cultivated variety known to possess this factor) it is proposed to designate this factor as "Rd_1". The variety Laggan also possessed the same gene. The two linked factors possessed by Garry for resistance to races 2, 10 and 12 were derived from Hajira and it is proposed therefore to designate them as "Hj_1" and "Hj_2". A recombination value of $26{\cdot}69 \pm 2{\cdot}29$ crossover units was calculated between these genes.

(B) *Studies on Crown Rust Resistance.*

(*a*) F_1 Reactions.

In Table 9 are given the reactions of the F_1 plants of the crosses of Garry when tested with different races of crown rust. The parental reactions are given below the F_1 reaction types. Reactions to the different races in the adult stage and in the field are also given in the table.

One seedling in the cross Burke × Garry tested against race 226 and two seedlings in the cross Garry × Joanette tested against race 203 did not show any infection. In other cases either full or partial dominance of resistance was noted in the seedling as well as the adult stage, with the exception of two seedlings of the cross Algerian × Garry and one seedling of the cross Fulghum × Garry. These three seedlings gave a moderately susceptible reaction of (2+) type.

(*b*) F_2 Segregation.

It was observed from the behaviour of certain progenies of F_1 plants in tests against stem rust that different genotypes operated, thereby indicating genetic diversity in different single plant selections of Garry. Seedling tests with different races of crown rust and field behaviour showed that all the F_2 progenies of F_1 plant nos. 5, 8 and 9 of the cross Fulghum × Garry and plant no. 19 of the cross Algerian × Garry were susceptible. In the seedling stage progenies of F_1 plant nos. 1, 7, 11 and 15 of the cross Fulghum × Garry and of F_1 plant nos. 1, 4 and 14 of the cross Algerian × Garry were all susceptible. Of these, however, plant nos. 4 and 14 of the latter cross and no. 15 of the former segregated for crown rust behaviour in the field. The data for seedling and adult plant tests are presented in Tables 10 and 11 respectively.

From the F_3 behaviour of certain F_2 plants reported later it was concluded that an inhibitor factor suppressed the dominant action of a factor for resistance and that these were linked with approximately 10% recombination. On this assumption and with the operation of another single factor, the expected ratio of resistant to susceptible plants was 3·2:1. Although the presence of the inhibitor group could not be ascertained in the progenies of all F_1 plants shown in the table, comparisons of observed and expected figures are based on its presence. It will be observed that a satisfactory fit to a 3·2:1 ratio was not obtained in all individual cases and was particularly very poor for the aggregate of all crosses. The overall ratio of R:S plants observed was 2·62:1, which was less than a monofactorial ratio and greater than a bifactorial ratio of complementary dominant factors. This suggested a linkage between two such complementary factors in coupling phase. A heterogeneity test gave a Chi-square value of

TABLE 9.

Reactions of F_1s and Parents Used in Crosses Involving Garry Tested Against Different Races of Crown Rust.

Parent or Cross.	Seedling Reactions to Races.		Adult Plant Reactions to Races.				Field.
	203	226	203	226	237	237–4	
Algerian × Garry ..	—	3/5 (1n) 2/5 (2+)	—	—	—	—	—
Fulghum × Garry ..	—	3/4 (1n) 1/4 (2+)	—	—	—	—	—
Burke × Garry ..	2/2 (3c)	1/4 (0) 1/4 (1n) 2/4 (1+n)	—	—	—	—	4/4 R
Laggan × Garry ..	—	2/2 (3−c)	R	R	R	R	Int. R
Garry × Gothland ..	—	2/2 (2−n)	—	Int. R	Int. R.	—	—
Garry × Joanette ..	2/2 (0)	—	MR	MR	—	R	—
Garry	(1n)	(1n)	R	R	R	R	I (98%)
Other parents ..	(4)	(4)	S	S	S	S	S

12·38 for 20 degrees of freedom between individual segregations within crosses and of 3·69 for 5 d.f. between crosses. The probability was in no case less than ·5, indicating homogeneity of the data. In the last column of the table are given the probabilities for the different F_2 populations and totals based on the assumption of the action of two complementary dominant factors linked with a recombination value of 9·59%. This value was derived as later reported from the combined analysis of F_2 and F_3 data by the method of maximum likelihood. In no case was the probability less than ·10, indicating good agreement between observed and expected results.

Data on F_2 segregation in the field are given in Table 11.

It has been mentioned earlier that certain progenies of F_1 plants indicated the operation of the inhibitor group. With the operation, therefore, of an additional factor for adult plant resistance the expected ratio was 3·2:1 and with additional duplicate factors the expected ratio was 15·7:1. In the absence of the inhibitor group the expected ratio was 3:1 in the former case. In the seedling stage, plant nos. 4, 14 and 20 of the cross Algerian × Garry and plant no. 15 of the cross Fulghum × Garry did not show any resistant plants in their progeny tests, indicating the absence of the inhibitor and its linked factor. It will be observed from the table that these plants gave a number of resistant and intermediate type of resistant adult plants. Except for plant no. 15 of the cross Fulghum × Garry the other three indicated the operation of a gene for adult plant resistance. Plant nos. 2, 6, 13 and 18 of the cross Algerian × Garry, nos. 2, 4, 12 and 14 of the cross Fulghum × Garry and no. 3 of the cross Burke × Garry clearly indicated the operation of a factor for adult plant resistance in addition to the inhibitor group. Whereas plant nos. 16 and 17 of the cross Algerian × Garry indicated the operation of two factors for adult plant resistance, plant nos. 3 and 13 of the cross Fulghum × Garry showed a poor fit to the expected ratio of 15·7:1. There was an

excess of moderately susceptible plants. In this cross it will be observed, in general, that the number of highly resistant plants was lower in comparison with the other crosses. This indicated the probable operation of minor modifying factors. These assumptions were confirmed from the F_3 behaviour presented later.

(c) F_3 Breeding Behaviour.

To confirm the hypothesis of linked factors, random F_3 lines from the progenies of certain F_1 plants and also lines from classified F_2 material were tested to different races

TABLE 10.

Segregation for Crown Rust in the Progenies of Certain F_1 Plants of Crosses Involving Garry, Indicating the Operation of Two Linked Dominant Complementary Factors (Recombination Value, 9·59±1·68) and of an Inhibitor and its Linked Inhibited Dominant Factor (Recombination Value, approx. 10).

Cross and F_1 plant no.	Race Used.	F_2 Reaction.				Ratio of R : S.	Probability.	
		Res.	MR.	MS.	S.		3·2 : 1.	71·9 : 28·1.
Algerian × Garry								
2	226	124	18	23	21	3·2 : 1	0·5 –0·3	0·2 –0·1
	226	22	53	27		3·1 : 1	0·7 –0·5	0·8 –0·7
5	237–4	23	28	21		2·4 : 1	0·3 –0·2	0·95–0·9
6	226	42	—	12	4	2·6 : 1	0·5 –0·3	0·7 –0·5
	203	46	24	8	18	2·8 : 1	0·5 –0·3	0·7 –0·5
9	237–4	25	22	21		2·2 : 1	0·2 –0·1	0·7 –0·5
11	203	46	8	19	11	1·8 : 1	0·02–0·01	0·2 –0·1
12	237–4	131	3	39	11	2·7 : 1	0·3 –0·2	0·8 –0·7
	203	56	21	19	13	2·4 : 1	0·3 –0·2	0·8 –0·7
13	237–4	62	9	18	4	3·2 : 1	0·99–0·95	0·5 –0·3
16	203	29	23	16	10	2·0 : 1	0·05–0·02	0·5 –0·3
17	226	86	11	40	1	2·7 : 1	0·2 –0·1	0·7 –0·5
Total ..	..	912		356		2·6 : 1	0·01–0·001	0·95–0·9
Fulghum × Garry								
2	226	47	4	10	14	2·1 : 1	0·1 –0·05	0·5 –0·3
3	203	85	41	32	16	2·6 : 1	0·3 –0·2	0·9 –0·8
10	226	11	43	20	5	2·2 : 1	0·1 –0·05	0·5 –0·3
	237–4	17	18	19		1·8 : 1	0·1 –0·05	0·3 –0·2
Total ..	..	266		116		2·3 : 1	0·01–0·001	0·5 –0·3
Burke × Garry								
1	203	183	27	42	32	2·8 : 1	0·5 –0·3	0·5 –0·3
2	226	43	73	4	44	2·4 : 1	0·2– 0·1	0·8 –0·7
	203	38	73	37		3·0 : 1	0·8 –0·7	0·5 –0·3
3	237	142	2	45	2	3·1 : 1	0·8 –0·7	0·3 –0·2
Total ..	..	581		206		2·8 : 1	0·2 –0·1	0·3 –0·2
Laggan × Garry								
3	203	127	23	59		2·5 : 1	0·3 –0·2	0·95–0·9
4	203	64	108	71		2·4 : 1	0·05–0·02	0·8 –0·7
Total ..	..	322		130		2·5 : 1	0·02–0·01	0·8 –0·7
Garry × Gothland								
1–6	226	16	81	28		3·5 : 1	0·7 –0·5	0·2 –0·1
	203	7	126	5	47	2·6 : 1	0·3 –0·2	1·0 –0·99
Total ..	..	230		80		2·9 : 1	0·5 –0·3	0·5 –0·3
Garry × Joanette								
4	226	14	—	3	—	4·7 : 1	0·7 –0·5	0·5 –0·3
1–4	203	56	10	1	22	2·9 : 1	0·7 –0·5	0·7 –0·5
Total ..	..	80		26		3·1 : 1	0·95–0·9	0·5 –0·3
Grand total	..	2391		914		2·62 : 1	<0·001	0·7 –0·5

in the seedling and in the adult plant stages. The observations on F_3 reactions are presented in Tables 12 and 13. Some lines in each cross showed the presence of moderately resistant plants in the resistant, segregating and susceptible lines. When such plants were found in the susceptible class the reaction was indicated as S:R. The expected behaviour indicated a ratio of 20·53 (R & R, R⁻) : 51·35 (R, R⁻, S & R⁻, S) : 28·11 (S, R⁻ & S) in the seedling stage.

TABLE 11.

F_2 Segregation for Crown Rust in the Field in the Progenies of Certain Crosses Involving Garry.

Cross and F_1 plant no.	Field Reactions.			Total.	Expected Ratio.	Probability. (Chi-square.)
	Resistant.	Intermediate.	Susceptible.			
Algerian × Garry						
2	12	159	38	209		
6	5	18	9	32		
13	1	1	1	3		
18	2	10	3	15		
Total	208		51	259	3·2 : 1	0·2– 0·1 (2·44)
4	12	97	27	136		
14	17	41	11	69		
20	7	12	8	27		
Total	186		46	232	3·0 : 1	0·1-0·05 (3·31)
16	2	8	0	10		
17	9	38	3	50		
Total	57		3	60	15·7 : 1	0·8–0·7 (0·106)
Fulghum × Garry						
2	—	9	6	15		
4	—	3	1	4		
12	6	133	46	185		
14	3	36	9	48		
Total	190		62	252	3·2 : 1	0·8–0·7 (0·088)
3	—	11	12	23		
13	9	42	27	78		
Total	62		39	101	15·7 : 1	<0·001
15	2	113	70	185	3·0 : 1	<0·001
Burke × Garry						
3[1]	83	108	60	251	3·2 : 1	0·99–0·95 (0·0009)

[1] This cross was tested in the winter of 1954, whilst others were tested in 1953 winter.

In Table 12 wherever tests were carried out with more than two races the same F_3 lines were tested. In the above tests the ratio ranged between 2·3 to 3·5 segregating lines for each resistant line. The average for all lines was 1 resistant : 2·9 segregating. For a single major gene segregation the expected ratio was 1:2. The observed ratio was greater than this and less than 1:8, as expected for complementary factor pair segregation.

It will further be observed that certain lines showed segregation with the majority of plants susceptible. The reactions in the F_3 lines derived from random F_2 plants of F_1 plant 8 of the cross Fulghum × Garry when tested against race 226 showed that out of 58 lines none were fully resistant and only four segregated with a preponderance of resistant plants. Twelve lines were S:R and the remainder gave a susceptible reaction. Lines showing a majority of resistant plants indicated the operation of a dominant

factor for resistance, and S:R segregation either a recessive factor for resistance or an inhibitor factor for the dominant factor mentioned above. The operation of the latter was considered to be more likely. If it is assumed that the inhibitor factor was independent of the dominant factor an F_3 behaviour of 1R; 2R:S; 6S:R; 7S was expected in the progenies of F_1 plant no. 8. Out of 58 lines tested none were resistant and only 4, as against 7 expected, were found to segregate R:S. Among the lines segregating S:R one-third were expected to segregate 3S:1R. Of the 12 lines of this class three lines were found to segregate 3:1. A critical examination of the lines derived from susceptible F_2 plants revealed that out of 190 lines classified as S:R or S, 42 lines segregated S:R and of these 15 lines gave a 3:1 ratio (this excludes the data from the crosses of Garry with Laggan and Burke, which were studied later). Instead of obtaining a 13S:3R ratio

TABLE 12.

Crown Rust Reactions of F_3 Lines in the Seedling Stage Indicating Operation of Linked Genes in Various Crosses Involving Garry.

Cross and F_1 plant no.	Race Used.	F_3 Reactions.						Total.	P Value (greater than).
		Resistant.	R, R^-.	R, R^-, S.	R^-, S.	S : R^-.	Susceptible.		
Algerian × Garry									
2	226	19	10	88	4	1	35	157	0·1
	203	29	6	82	8	1	34	160	0·2
6	Field collection	6	9	53	—	3	21	92	0·3
17	Do	—	8	24	1	2	8	43	0·5
Fulghum × Garry									
2	203	2	12	25	11	13	15	78	0·2
	286	2	11	32	6	11	17	79	0·3
3	203	11	2	43	3	11	12	82	0·5
	226	3	9	35	—	9	11	67	0·8
	286	5	6	34	3	5	14	67	0·5
4	203	11	3	30	2	4	10	60	0·5
	226	2	10	27	5	3	13	60	0·95
	286	6	5	25	5	2	14	57	0·95
Laggan × Garry									
8[1]	226	—	—	4	—	12	42	58	0·3
1[2]	203	6	8	10	9	6	26	85	0·2
Burke × Garry									
3[2]	230	51·6		125·1		74·3		251	0·8

[1] Expected segregation in this plant was 0·25 (R) : 5·0 (R : S) : 45·0 (S : R) : 49·75 (S).

[2] Random lines and/or lines from F_2 progenies classified in the field were used. The data on these crosses were not utilized in calculating the linkage values.

in the other lines, only 1 or 2 resistant plants were noted amongst about 20 plants per line. The number of susceptible lines observed was far greater in proportion to the segregating lines, when compared with the expected proportion of 7 out of every 13. In all, 95 lines gave a S:R reaction to one or other race, and of these only 15 lines segregated S:R to all four races 203, 226, 237–4 and 286.

A further study of 159 lines from the F_1 families of plants 4 and 14 of the cross Algerian × Garry and of plants 5 and 15 of the cross Fulghum × Garry did not show any resistant plant in any lines except for two plants in each of two lines. This clearly excluded the possibility of natural crossing as an explanation for the occurrence of 1 in 20 plants as resistant. Calculations based on the occurrence of 15 lines segregating approximately 3S:1R, and 31 out of 95 lines segregating to any one of the four races and also on the segregation observed in the F_3 of the progeny of F_1 plant 8 of the cross Fulghum × Garry, indicated an approximate linkage value of 10 units between the inhibitor factor and the dominant gene it inhibited. Calculating the expected F_3 behaviour on this assumption would give 0·25 line resistant, 5·0 lines segregating R:S, 4·5 lines segregating 3S:1R, 40·5 lines segregating with 1 resistant plant in about 20 and 49·75 lines fully susceptible. The lines showing 1 in 20 plants as resistant may not

be observed to be segregating in tests against all the races. The F_3 behaviour observed in plant 8 of the cross Fulghum × Garry fitted closely the expectation with a probability value greater than ·3.

The data in F_2 and F_3 studies in the seedling stage indicated linkage between two complementary dominant factors and in calculating the recombination value of these factors the above observations were considered. The combined logarithmic likelihood expression for the F_2 and F_3 data thus derived was: $2391 \text{ Log.}(1221-758p+379p^2) + 1050 \text{ Log. } 379\ (1+2p-p^2) + 91 \text{ Log.}(403-758p-399p^2) + 286\ (818+40p-20p^2)$.

The classes S:R and S for F_3 reactions were combined. Maximization with respect to "p" gave a value of ·0959 ± ·0168. Thus a recombination value of 9·59% ± 1·68% was obtained.

In the F_2 the ratio of resistant to susceptible seedlings was 71·9:28·1 on this basis and in the F_3 20·5:51·4:28·1 for resistant : segregating : susceptible lines. The susceptible class included lines segregating S:R, with a preponderance of susceptible plants. All the individual single F_1 plant progeny segregations obtained in F_2 and F_3 showed good agreement. In the F_2 the various Chi-square values were: (*a*) for deviation 0·3445 (1 d.f.), (*b*) for heterogeneity within crosses 10·718 (20 d.f.) and (*c*) for heterogeneity between crosses 3·6704 (5 d.f.). Probability of chance deviation in every case was not less than 50%, indicating good agreement between observed and expected results and homogeneity of the data.

The behaviour in the field of certain F_1 plant progenies is given in Table 13.

TABLE 13.

Adult Plant Behaviour of Certain F_3 Lines in the Crosses Algerian × Garry and Fulghum × Garry at Castle Hill Farm in 1954.
(Expected values in brackets.)

Cross and F_1 plant no.	F_2 Reactions.						Expected Ratio.	Probability.
	R.	R, R^-.	R, R^-, S.	R^-, S.	S : R^-	S.		
Algerian × Garry								
2	15	28	74	4	22	6		
6	4	14	32	—	14	2		
Fulghum × Garry								
2	6	6	28	3	14	6	25·2 : 51·2 : 23·6	
4	5	7	23	5	1	10		
Total	85 (83·4)		169 (169·9)		78 (78·7)			0·9–0·8
Algerian × Garry								
11	6	4	11	2	1	—		
17	16	43	71	6	6	3	43·8 : 50·2 : 5·9	
Fulghum × Garry								
3	29	22	55	9	5	7		
Total	120 (127·7)		159 (146·0)		22 (17·3)			0·3–0·2

It will be observed from Table 13 that also in the field certain F_2s from these F_1 plants gave progenies which segregated with a preponderance of susceptible plants. This indicated that the inhibitor factor and its linked dominant factor for resistance were operative in the field also. In the table it again will be seen that F_3 families of some F_1 plants indicated the operation of a single major factor for adult plant resistance whilst others suggested duplicate factors. These results substantiated some of the observations made in F_2 on adult plants. Due to the operation of the inhibitor group the ratio of 1:2:1 or 7:8:1 was changed slightly as indicated in the table. The probability values were greater than ·8 for monogenic segregation and greater than ·2 for the duplicate factor segregation, indicating a good fit. The S:R class was included with the susceptible class. When the expectancies were calculated with the S:R class taken separately, the probability values were greater than ·02 in the former and greater than ·3 in the latter case.

In the summer of 1955, 278 lines from the crosses Algerian × Garry (F_1 plant nos. 4 and 14), Fulghum × Garry (F_1 plant no. 15) and Burke × Garry (F_1 plant no. 1) were sown in the field, but due to the predominance of race 259 all the lines gave a susceptible reaction.

(*d*) Relationship of Reactions to Different Races.

F_2 plants classified to one race were studied for their F_3 behaviour to the same or a different race. The breeding behaviour is presented in Table 14.

It will be observed from the data presented in Table 14 that F_3 lines derived from resistant F_2 plants were either fully resistant or segregated with a preponderance of resistant plants. Similarly the lines derived from the susceptible F_2 plants were either susceptible or segregated with susceptible plants preponderant, except for one line which was fully resistant. In the intermediate classes, however, several lines were

TABLE 14.

F_3 Breeding Behaviour of the Progenies of Classified F_2 Plants in the Seedling Stage.

F_2 Reactions to Race.	F_3 Reactions to Race.				Total.
	Resistant.	Segregating R : S.	Segregating S : R.	Susceptible.	
226		203			
R	3	19	—	—	22
MR	2	6	—	1	9
MS	1	—	5	20	26
S	—	—	—	1	1
203		Composite field inoculum			
R	10	31	—	—	41
MR	3	17	—	1	21
MS	—	4	1	7	12
S	1	—	2	12	15
203		203			
R	13	22	—	—	35
MR	2	6	3	4	15
MS	1	1	1	2	5
S	—	—	—	10	10
203		226			
R	14	17	—	—	31
MR	4	6	—	—	10
MS	2	4	1	—	7
S	—	—	—	5	5

found to behave differently from the expected ratio. Nine lines from the MR F_2 reaction type class gave lines that were either susceptible or segregated with a preponderance of susceptible plants and, similarly, 14 lines derived from MS plants gave fully resistant progenies or segregating R:S progenies. This aberrant behaviour of certain F_2 plants of the intermediate classes, particularly to the same race in F_3, indicated errors in classification or labelling. Corrections in the F_2 data were made on this basis wherever possible.

F_3 seedling vs. F_3 seedling comparison to different races is presented in Table 15.

It will be seen from reactions presented in Table 15, for behaviour against paired races, that the majority of lines gave identical reactions. Four hundred and eighty-two lines gave resistant and segregating reactions to both races and only 17 gave a resistant reaction to one race but segregated to the other. Twelve lines showing segregation gave either a S:R behaviour or were homozygous susceptible to the other race. These

discrepancies suggested some errors in classification. From among the susceptible and S:R lines 181 gave identical reactions and 35 gave a S:R reaction to one race, but were susceptible to another. In the S:R class, as already mentioned, it was expected that certain lines would give about 1 in 20 plants with a resistant reaction. Such lines may not have shown identical reactions to the paired races and, as such, the observed behaviour of these lines was not unexpected. In general, analysis of reactions clearly indicated that the same factors conditioned resistance to races 203, 226, 237, 237–4 and 286.

Seedling reactions vs. adult plant reactions: Relationship between seedling reactions and adult plant reactions were studied in the F_2 of the cross Garry × Gothland, between

TABLE 15.

Relationship of F_3 Behaviour to Different Races of Crown Rust in Certain Crosses Involving Garry.

F_4 Reactions to Race.	F_3 Reactions to Race.			
	Resistant.	Segregating R : S.	Segregating S : R.	Susceptible.
203		226		
Resistant	73	11	—	—
Segregating				
(R : S)	2	199	1	4
(S : R)	—	2	19	16
Susceptible	—	2	2	74
286		226		
Resistant	37	1	—	—
Segregating				
(R : S)	1	106	1	—
(S : R)	—	1	9	6
Susceptible	—	1	7	47
203		237–4		
Resistant	7	1	—	—
Segregating				
(R : S)	1	21	—	—
(S : R)	—	—	24	3
Susceptible	—	—	1	7
203		237		
Resistant	10	—	—	—
Segregating				
(R : S)	—	28	—	—
(S : R)	—	—	1	—
Susceptible	—	—	—	—

adult plant reactions in the F_2 and seedling reactions in the F_3 in the cross Burke × Garry and between F_3 reactions in the two stages in the cross Fulghum × Garry and Algerian × Garry. The appropriate data are presented in Tables 16 and 17.

In Table 16 the expected frequencies of the susceptible class, indicated in brackets, were calculated on the assumption that two factors conditioned adult plant resistance in this cross with one showing linkage with the two complementary factors for seedling resistance, approximately 10 units away from the gene proximal to it. This inference was obtained from F_3 studies in the seedling as well as adult stage of the same lines. The data are presented in Table 17.

In the cross Burke × Garry 201 lines were studied from an F_2 population of 251 plants classified in the adult stage in the field for crown rust behaviour; therefore the observed frequencies in the table were adjusted on the basis of the original F_2

TABLE 16.

Relationship between F_2 Seedling and Adult Plant Reactions in the Cross Gothland × Garry. (Expected values in brackets.)

Adult Plant Reactions.	Seedling Reactions.			Total.
	Resistant.	MR.	Susceptible.	
Resistant	32	24	13	69
MR	—	—	1	1
MS–S	— (1·1)	—	9 (3·8)	9 (4·8)
Probability[1] ..	0·7–0·5		0·01–0·001	0·1–0·05

[1] Yates' correction factor applied.

TABLE 17.

Relationship between Adult Plant Reactions and Seedling Reactions in F_3 in Certain Crosses Involving Garry. (Expected values in brackets.)

Cross and F_1 plant no.	Adult Plant Reactions.	Seedling Reactions in F_3.				Total.
		Resistant.	Segregating (R : S).	Segregating (S : R).	Susceptible.	
	F_2					
(*a*) Burke × Garry	Resistant ..	50·2 (51·1)	111·2 (116·7)	29·6 (23·8)		191 (191·6)
	Susceptible ..	1·4 (0·48)	13·9 (12·2)	44·7 (46·7)		60 (59·4)
	Total ..	51·6 (51·6)	125·1 (128·9)	74·3 (70·6)		251
	Seedling (F_3).	Adult plant reactions (F_3) (indicating the operation of one factor for adult plant resistance)				
(*b*) Algerian × Garry F_1 plant nos. 2 and 6 and Fulghum × Garry F_1 plant nos. 2 and 4	Resistant ..	44 (48·0)	7 (10·9)	0 (0·56)	0	51 (59·5)
	Segregating (R : S) ..	29 (22·5)	123 (112·3)	5 (14·1)	1	158 (148·9)
	(S : R) ..	1	2	8	6	
	Susceptible ..	1	13	30	20	81
		(2·3)	(25·2)	(54·0)		(81·5)
	Seedling (F_3).	Adult plant reactions (F_3) (indicating the operation of two factors for adult plant resistance)				
(*c*) Algerian × Garry F_1 plant no. 17 and Fulghum × Garry F_1 plant no. 3	Resistant ..	37 (39·1)	10 (6·6)	1 (0·1)	0	48 (45·8)
	Segregating (R : S) ..	34 (41·6)	69 (70·1)	1 (2·7)	0	104 (114·4)
	(S : R) ..	4	13	0	1	
	Susceptible ..	9	26	8	10	71
		(17·0)	(35·3)	(10·4)		(62·7)
			(*a*)	(*b*)	(*c*)	
Chi-square for seedling reactions			0·3 (P= 0·9 –0·8)			
Chi-square for adult plant reactions			0·003 (P= 0·99–0·9)			
Chi-square for association			2·39 (P= 0·8–0·7)	15·3 (P= 0·1–0·05)	12·8 (P= 0·2–0·1)	

frequencies. It will be observed from the behaviour of the classified plants that the majority of plants classified as resistant gave either fully resistant F_3 lines or gave lines segregating R:S. Several lines were also susceptible. Similarly, from susceptible F_2 plants the majority of the lines derived were susceptible and a few lines were either fully resistant or were segregating R:S. Observations made on the F_3 lines in the two stages also indicated similar patterns. A test of independence clearly indicated association between seedling resistance and adult plant resistance since the probability was less than ·001 in every case.

If it is assumed that one of the two factors for seedling resistance governed adult plant resistance as a single dominant factor, then from the class of lines segregating R:S in Table 17 (*b*), 9% or only 14·2 lines were expected to be homozygous resistant in the field. The observed number was 29. Similarly from the lines susceptible in the seedling stage 1% or 0·89 line would be resistant and 9·6% or 7·9 lines segregating. The observed numbers were 2 and 15 respectively. The deviations were therefore large. Similar deviations were noted in the other two parts of the table.

An alternate assumption on the basis of another factor linked with the two complementary factors for seedling resistance and showing approximately 10% crossing over offered a more satisfactory explanation and gave closer fits to the expected frequencies. Expected frequencies on the basis of this assumption are shown below.

Seedling Reactions in F_3, Indicating the Operation of IVc_2 Vc_2 and Vc_a Vc_b	Adult Plant Reactions in F_3 (Indicating the Operation of IVc_2 Vc_2).						Total.
	And single dominant factor linked with seedling resistance.			And two dominant factors, one linked with seedling resistance.			
	Resistant.	Segregating (R : S).	Susceptible including S : R.	Resistant.	Segregating (R : S).	Susceptible including S : R.	
Resistant ..	16·556	3·784	0·191	17·550	2·944	0·048	20·53
Segregating ..	7·769	38·728	4·851	18·664	31·472	1·213	51·35
Susceptible (including S : R)	0·803	8·678	18·630	7·630	15·826	4·658	28·11
	25·128	51·190	23·670	43·844	50·242	5·919	100·00

For calculating the F_2 frequencies the resistant and the segregating classes are combined.

The data presented in Tables 16 and 17 show a close fit to the expected frequencies, calculated from the figures given above. In Table 17 (*b*) the deviation was not significant at the 5% level of significance. In the cross Garry × Gothland (Table 16) two factors for adult plant resistance operated and in the cross Burke × Garry only the factor linked with the complementary factors for seedling resistance operated. In the latter cross 11 lines in the susceptible class of F_3 reactions were found to give a S:R reaction.

The recombination value was assumed to be approximately 10% because the segregating ratios to the different races in the seedling stage varied slightly and a very accurate estimation was not possible.

(*e*) Designation of Factors for Crown Rust Resistance.

On the basis of the scheme for gene designation outlined earlier, the complementary factors were designated Vc_a and Vc_b, the dominant factor as Vc_2 and its inhibitor as IVc_2. The two factors for adult plant resistance were designated $V\bar{c}_1$ and $V\bar{c}_3$, $V\bar{c}_1$ being linked with the two complementary factors thus: $\frac{Vc_a \quad Vc_b \quad V\bar{c}_1}{9{\cdot}59 \pm 1{\cdot}68 \quad 10 \text{ approx.}}$. Vc_2 and IVc_2 were also 10 units apart.

(C) *Relationship between Factors for Stem Rust Resistance and Crown Rust Resistance.*

Chi-square values were calculated for independence of crown rust reactions and stem rust reactions in the F_2 and F_3 generations involving the different factors. A tabular statement of the information is presented in Table 18. Since Vc_a, Vc_b and $\bar{Vc_1}$ were linked as were Hj_1 and Hj_2, independence was calculated for only one of the factors in each case.

The test for independence of stem rust resistance and crown rust reactions clearly indicated their independent inheritance, both in seedling and adult plant tests.

TABLE 18.

Chi-square Test for Independence of Stem Rust and Crown Rust Resistant Factors.

Generation Studied.	Factors.	N.	D.F.	Probability.
F_2	$Hj_1\ Hj_2$ vs. $Vc_a\ Vc_b\ Vc_1$, IVc_2Vc_2	106	2	0·2 –0·1
F_3	As above	596	6	0·5 –0·3
F_3	Rd_1 vs. as above	22	6	0·98–0·95
F_3	Rd_1, $Hj_1\ Hj_2$ vs. $\bar{Vc_3}$	36	6	0·5 –0·3
F_2	Hj_1 or Hj_2 vs. $\bar{Vc_1}$	251	1	0·99–0·95

DISCUSSION.

The variety Garry, when tested as seedlings to different races or in the field, showed heterogeneity. The fact that this was not due to mechanical mixture was evident from the present studies. The heterogeneous character of Garry was particularly expressed in its crosses with Algerian and Fulghum in the F_1, F_2 and F_3 generations. Twenty F_1 progenies of the cross Algerian × Garry, 15 of the cross Fulghum × Garry, 4 of the cross Burke × Garry, 4 of the cross Laggan × Garry, 6 and 5 respectively of the crosses Gothland × Garry and Joanette × Garry were utilized in the present studies. Due to the heterogeneous nature of the parent Garry, certain F_1 plants and/or their progenies differed in behaviour to both stem rust and/or crown rust races.

In the present studies three factors were identified conditioning stem rust resistance. One common factor in Garry and Burke (and indirectly Laggan) conditioned resistance to races 2 and 12. This factor was possibly the same as that in Richland and reported by workers in other countries. The other two factors were found linked with a recombination value of 26·69 ± 2·29 and conditioned resistance against races 2, 10 and 12. Workers in North America identified four factors, derived from the variety Hajira, in Garry or its sister selections. One was the same as the Richland factor, two independent factors conditioned resistance to race 8 (a race closely allied to race 10) and one was similar to the Richland factor except that it did not condition resistance to race 7A. Probably one of the two linked factors against Australian races was identical with one of the factors conditioning resistance to race 8 in North America. The present investigations, therefore, added one more factor to the gene pool of sources of resistance to stem rust.

Waterhouse (unpublished) studied crosses of R.L.1692 (Garry O.259) with Fulghum, Algerian and Adonis and studied the segregation to stem rust races 2, 7 (allied to race 12) and 8 (allied to race 10). A population of 1,054 F_2 plants from 20 different F_1 plants, studied against races 2 and 7, showed 46 susceptible. A fit to the ratio of 96·64:3·36 shows no significant deviation at the 5% level of probability. From 484 plants studied for behaviour to race 10, 93 were susceptible. An excess of 28·5 plants was therefore shown in the susceptible class in this case, indicating a significant deviation. However, it was noted that some of the F_1 progenies gave a good fit to the expected ratio of 86·6:13·4 and that the over-all ratio of 4·2:1 indicated an intermediate ratio between monogenic and digenic segregation. The operation of linked factors was thus suggested.

These crosses were made in 1946 and 1948 and the crosses of the same Accession Number O.259 with Fulghum and Algerian made in 1951 were studied by the present authors.

The studies on crown rust inheritance in Garry revealed its complicated nature against Australian races. In all, six factors were identified. Two major dominant complementary linked factors conditioned seedling resistance only and similarly two independent factors conditioned adult plant resistance only. An additional factor conditioned resistance both in the seedling and in the adult plant stage. The resistance due to this factor was, however, inhibited by the action of another gene linked with it and separated by approximately 10 crossover units. One of the genes for adult plant resistance was further found linked with the two complementary factors for seedling resistance. No previous report has been made of linkage between the factors of the Victoria type. Usually only a single factor has been reported or wherever more than one factor was reported (e.g., Welsh *et al.*, 1953) the factors were considered independent. The identification of the numerous factors for crown rust resistance in Garry was made possible because of different types of segregation in the progenies of different F_1 plants. Progenies of 54 F_1s were studied. Some of them possessed factors for resistance to stem rust only, others to crown rust only. Again, among these types, some showed segregation of one or both factors for seedling resistance and others for factors for adult plant resistance. The identification of the factor inhibiting the action of a dominant factor would not have been possible except for the F_3 segregation of these factors only in the progeny of F_1 plant number 8 of Fulghum × Garry, where these two factors were also indicated as linked.

The results with the Australian races differed greatly from those where the same races (on the conventional international set designation) of another country were used. This indicates that the identification of the races on the international set of differentials does not necessarily help in the utilization of information available for resistance against any particular race in another country. This is in agreement with observations made by Watson and Waterhouse (1949) concerning race 34 of wheat stem rust.

The results indicated that the factors conditioning seedling resistance did not confer resistance against the same races in the field. This was clear from the F_3 studies carried out using composite inoculum collected from the field for seedling tests in the glasshouse. The factors for seedling resistance operated against this inoculum in the usual manner and the reactions were identical with those when race 203 was used in the seedling stage. In the field, however, two different factors conferred resistance. These observations make it necessary for the breeder to study his breeding material carefully before incorporating resistance into any economic variety.

The fact that a single race, 259Anz.1, made all the factors for crown rust resistance in Garry and Victoria ineffective stresses the need for introducing more factors for crown rust resistance from diverse sources. Studies assessing the possibility of introducing diverse genes into Garry or Victoria have been carried out by the senior author and will be reported in a series of subsequent papers.

Summary.

Studies on the inheritance of stem rust resistance and crown rust resistance were carried out in various crosses involving the variety Garry. It was clear that Garry was a heterogeneous mixture of types. Studies on the progenies of 54 F_1 plants from the crosses of Garry with Algerian, Fulghum, Burke, Laggan, Gothland and Joanette revealed the operation of the following six factors for crown rust resistance and three factors for stem rust resistance:

$\frac{Vc_a \quad Vc_b \quad \bar{Vc_1}}{9{\cdot}59 \pm 1{\cdot}68 \quad 10 \text{ approx.}}$ in linkage group 1. Vc_a and Vc_b were complementary factors for seedling resistance to races 203, 226, 230, 237, 237–4 and 286. $\bar{Vc_1}$ conditioned adult plant resistance only.

$\frac{Vc_2\ IVc_2}{10\ \text{units}}$ in linkage group 2. Vc_2 conditioned seedling as well as adult plant resistance, but was inhibited by IVc_2.

$V\bar{c}_2$—independent dominant factor for adult plant resistance only.

Rd_1—independent factor for resistance to races 2 and 12 of stem rust.

$\frac{Hj_1\ \text{and}\ Hj_2}{26{\cdot}69 \pm 2{\cdot}29}$ in linkage group 3 conditioning seedling resistance to races 2, 10 and 12 of stem rust and field resistance.

The factors for crown rust resistance were independent of the factors for stem rust resistance.

Acknowledgement.

The F_1 plants of the crosses of Garry with Algerian and Fulghum and the crossed seeds of the cross Burke × Garry were kindly made available by Professor W. L. Waterhouse.

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